FORAGING BEHAVIOUR OF FOREST BIRDS OF THE DRY INTERIOR DOUGLAS-FIR, PONDEROSA PINE FORESTS OF BRITISH COLUMBIA

K.H. Morgan
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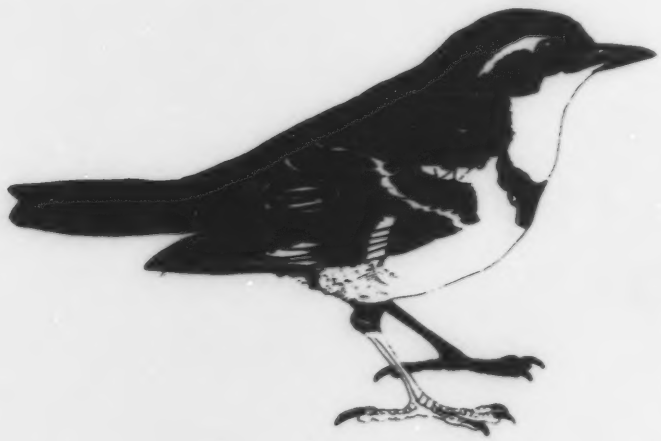

TECHNICAL REPORT SERIES No. 149
Pacific and Yukon Region 1991
Canadian Wildlife Service

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Technical Report Series No. 149
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This series may be cited as:

Morgan, K.H., J-P.L. Savard and S.P. Wetmore.
Foraging Behaviour of Forest Birds of the Dry Interior
Douglas-Fir, Ponderosa Pine Forests of British Columbia.
Technical Report Series No.149. Canadian Wildlife
Service, Pacific and Yukon Region, British Columbia.

Printed on recycled paper

Issued under the Authority of the
Minister of Environment
Canadian Wildlife Service

©Ministry of Supply and Services Canada 1991
Catalogue No. CW69-5/149E
ISBN 0-662-19506-X
ISSN 0831-6481

Copies may be obtained from:
Canadian Wildlife Service
Pacific and Yukon Region
P.O. Box 340,
Delta, British Columbia
Canada V4K 3Y3

Printed on recycled paper

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ABSTRACT

The foraging behaviour of 10 species of forest birds was studied from May through July of 1983 - 1986 at two locations in the dry interior Douglas-fir (*Pseudotsuga menziesii*) and Ponderosa Pine (*Pinus ponderosa*) forests of British Columbia. All bird species displayed highly variable foraging behaviours, although preferred feeding methods were discernable. Those forest structures that were quantified (eg. number of stems by species, diameter, and height) were not used in proportion to their availabilities; rather each species of bird partitioned the resources. Morphologically similar species of birds exhibited the highest levels of niche overlap in their exploitation of the forest resources. Competition for those resources may have occurred between like-species, but could not be demonstrated. The results of this study suggested that the vertical foraging location and the actual method of acquiring food (eg. pecking, probing etc.) were the two most important means of partitioning the habitat. Alterations, brought about by logging activities, in forest plant composition and/or structure, did not lead to significant changes in foraging behaviour of most species. In contrast, differences in (species-specific) foraging behaviours between the two study areas, were far more obvious. This may have been in response to between area differences in vegetation structure and/or composition; or in type, quantity, distribution and availability of invertebrate prey.

RÉSUMÉ

Entre 1983 et 1986, nous avons étudié le comportement alimentaire de 10 espèces d'oiseaux forestiers à deux sites localisés dans la zone biogéographique du Sapin Douglas (*Pseudotsuga menziesii*) et du Pin de Ponderosa (*Pinus ponderosa*), à l'intérieur de la Colombie-Britannique. Bien que toutes les espèces aient eues des comportements alimentaires très variables, on pouvait décerner des préférences comportementales. Les structures de l'habitat que nous avons mesuré (ex: nombre de tiges, diamètre et hauteur) n'étaient pas utilisées selon leur disponibilité mais plutôt partitionnées parmi les espèces. Il y avait un plus

grand chevauchement dans la niche alimentaire chez les espèces de morphologie semblable. Il est possible que ces espèces aient été en compétition, mais cela n'a pu être démontré. Nos résultats suggèrent que la hauteur au dessus du sol et la méthode d'acquisition de nourriture sont les deux moyens les plus importants de diviser l'habitat entre les espèces. Des modifications de la composition et de la structure végétale forestière n'ont pas amené de changements significatifs dans le comportement alimentaire de la plupart des espèces. Au contraire, les différences dans le comportement alimentaire d'une espèce donnée étaient plus évidentes entre les deux régions étudiées. Ceci était peut être en réponse aux différences dans la structure et/ou composition de la végétation entre les deux endroits, ou à des différences dans le type, l'abondance, la distribution et la disponibilité des proies.

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1. INTRODUCTION.

1.1. An Overview of Foraging Behaviour.

It has long been recognized that the densities and behaviours of birds within a given habitat are regulated by many interacting factors. Much attention has been directed towards the relationships between the structural complexity of the vegetation and the avian community. Some of the earliest studies examining the relationships between habitat structure and avian community population levels and species composition, include Johnston and Odum (1956), Bond (1957), MacArthur (1958, 1964), MacArthur and MacArthur (1961), and Karr and Roth (1971).

According to Morse (1990) "The study of food exploitation, including foraging (searching and selecting) has been a major preoccupation of avian ecologists and behavioralists over the last 35 years." As a result of this long-standing research focus, much insight has been gained into the complex relationships between bird species; prey (types, distribution and abundance); and plant morphology and community structure. It is beyond the scope of this paper to address all of the observed relationships that determine and/or modify an individual or species' foraging behaviour. However, we feel that in order to assess the results of this study, the major topics should be addressed. For more comprehensive overviews of these topics, as well as the current direction of research, we refer the reader to Morse (1989), Wiens (1989) and Morrison *et al.*(1990).

MacArthur's (1958) classic study of the foraging behaviours of coexisting, spruce-woods *Dendroica* warblers was the impetus for many subsequent feeding studies. MacArthur found that morphologically similar warbler species partitioned the available resources by means of differential foraging heights. This reduced competitive interactions, and permitted multispecies coexistence. Although each species of warbler differed in its "favoured" foraging height, there was considerable overlap in their vertical distributions. Because arboreal habitats are diverse horizontally as well, a bird encounters greater substrate differences when moving about on a horizontal plane, than when merely feeding in the lower or upper parts of the crown (Morse 1989). Further subdivision of the

resources along a horizontal plane permitted a greater number of species to coexist (MacArthur 1958).

Morse (1989) observed that: "Foraging varies along several spatial parameters in the three-dimensional environment occupied by tree dwellers. The extent of an individual's vertical distribution is determined by the structural heterogeneity of a forest as well as its height. Such variation depends on the extent that the emergent vegetation, canopy, understorey, and herb or ground layers differ in representation and physical structure. In turn, the arthropod fauna harboured by the forest differs concordantly. Not only will an insectivore's food supply be affected by the prey's morphological and physiological attributes, but problems of capturing them will change in response to these attributes." Preferences for particular tree species may occur because the food resource is greater on the preferred tree species, or because the physical configuration of the branches and/or foliage allows the bird to more easily search for and capture prey items (Balda 1969, Holmes *et al.* 1979, Holmes and Robinson 1981).

Most passerines display a wide range of foraging manoeuvres, with the frequency of these manoeuvres differing among species. In broad terms, the range of foraging manoeuvres include: picking up prey underfoot (gleaning), hovering at the tips of branches, hawking for flying insects (flycatching), and pecking or probing beneath the substrate surface. The manoeuvres employed are determined in part by the characteristics of the habitat the birds occupy (Morse 1968, Holmes *et al.* 1979, Mauer and Whitmore 1981), the prey (type, location and activity level) (Balda 1967, 1969, Holmes *et al.* 1978), and morphological differences in bird species (Robinson and Holmes 1982, 1984). Arboreal feeders range from tip foragers, to trunk foragers; in between lie the majority of species, the foliage gleaners, birds that concentrate their activities in the midst of the vegetation (Morse 1989).

In describing the extent to which birds vary their foraging patterns, avian behaviouralists have utilized the terms *stereotyped* (birds that exploit resources in the same way regardless of conditions) and *plastic* (birds that exploit

resources in different ways as conditions change) (Morse 1980). Among spruce-woods warblers, there is an inverse ranking between dominance and plasticity (Morse 1976, Sabo and Holmes 1983). The effect that competition has on the foraging behaviour, distribution and ultimately the breeding densities of subordinate birds has been observed in both phylogenetically similar (Morse 1971, Cody 1978) and dissimilar species (Holmes *et al.* 1978, Sherry 1979, Morgan 1984).

Intersexual differences in foraging locations and/or methods have been observed in many species of birds including spruce-woods warblers (Morse 1968), vireos (*Vireonidae*, Williamson 1971) and nuthatches (*Sittidae*, McEllin 1979). Morse (1989) suggests several plausible explanations for these differences, including the following: "Since males in high-density populations seldom if ever feed their females on the nest, this pattern of spatial separation may be highly efficient for the females. With high intra- and interspecific population densities, a male's time can be completely taken up in territorial defense...". In a thick canopied deciduous forest, the most conspicuous area to display is beneath the dense vegetation. This concentrates most of the male's activities (and foraging) below where the females nests (Holmes 1986). Female warblers perform all of the incubation, and are not fed by their mates. Therefore, access to a nearby food source that is defended by but not depleted by the male, favours efficient foraging by the female and minimizes the risks of egg predation (Morse 1989).

The foraging pattern of an individual bird as well as the rate of foraging, may change over time (eg. Pinowski 1977, Martin 1985 and Martin and Karr 1990). To date, the most detailed study of how a species foraging changes throughout a day, is by Holmes *et al.* (1978). They observed that the frequency of flycatching by American Redstarts (*Setophaga ruticilla*) increased as the day warmed and insects became more active; and that the Redstarts foraged lower in the canopy as the numbers of low-flying insects increased. Balda (1967) suggested that because the uppermost portions of a tree receive early morning sunlight sooner than the remainder of the tree, insects in that section likely become active

earlier. It is assumed that active prey are easier to detect than inactive ones (Franzreb 1983a, Morse 1989).

Lastly, but likely of great importance, inclement weather may drastically alter a species' foraging behaviour (Morse 1989). For example, wet foliage dampens a bird's plumage quickly, reducing its insulatory capability. Consequently, species that normally forage on the outer portions of a branch, frequently focus their efforts on the inner parts of the limbs during wet periods. There are several ramifications to such shifts. The species that have altered their location are now foraging in a suboptimal manner, likely on prey that they seldom take, and their encroachment on the species that normally utilize the area, is taking place at a critical time. If the encroached species are socially subordinate, it is unlikely that they will be able to resist the intruders. Frequent events such as this could ultimately effect either the reproductive fitness of a species, or influence its distribution and/or territory size (Morse 1976, 1989).

1.2. Study Objectives.

Few Canadian studies examining the relationships between forest structure and bird population dynamics and/or foraging behaviour have been published. Those we are aware of include Schwab (1974), Des Granges (1980), Freedman *et al.* (1981), Morgan (1984), Wetmore *et al.*(1985) and Morgan and Freedman (1986). In response to this information shortage, in 1983 the Canadian Wildlife Service, began a study in the dry interior of British Columbia investigating the relationships between forest structure, logging techniques and bird communities.

Concurrent with that investigation was a study of the foraging behaviour of the most abundant breeding species. The objectives of that parallel study were:

i) to characterize the feeding methods of each bird species in multidimensional space;

ii) compare the foraging use of quantifiable habitat variables with their availabilities;

iii) identify species that showed the highest degree of foraging similarity (niche overlap);

iv) examine the influence of logging activities on niche overlap and foraging behaviour.

This report summarizes and interprets the results of the behavioural study.

2. STUDY AREA.

From May through July of 1983-1986 breeding bird surveys and foraging behaviour studies were conducted at two locations (Princeton and Merritt) in the interior of British Columbia (Fig. 1). The vegetation, soils and climatic features of both locations placed them within the Interior Douglas-fir Biogeoclimatic Zone. The Princeton sites were further categorized as being in the Dry Western Montane Interior Douglas-fir and the Dry Montane Spruce subzones, while the Merritt sites were typical of Dry Submontane Interior Douglas-fir, Very Dry Submontane Douglas-fir and Very Dry Northern Ponderosa Pine-Bunchgrass subzones (Mitchell and Green 1981).

The Princeton study area was composed of three plots approximately 20km south of Princeton. Sites 1 and 2 had been logged during the winter of 1979/1980 following the diameter limit cutting technique. As the name implies, a minimum trunk diameter is set prior to timber extraction. Site 1 was lightly cut, with a minimum size limit of 40cm diameter at stump height (DSH) for all Douglas-fir (*Pseudotsuga menziesii*) and Ponderosa Pine (*Pinus ponderosa*). A minimum diameter of 15cm was set for all other species (primarily Trembling Aspen (*Populus tremuloides*), Lodgepole Pine (*Pinus contorta*) and Englemann Spruce (*Picea engelmannii*)).

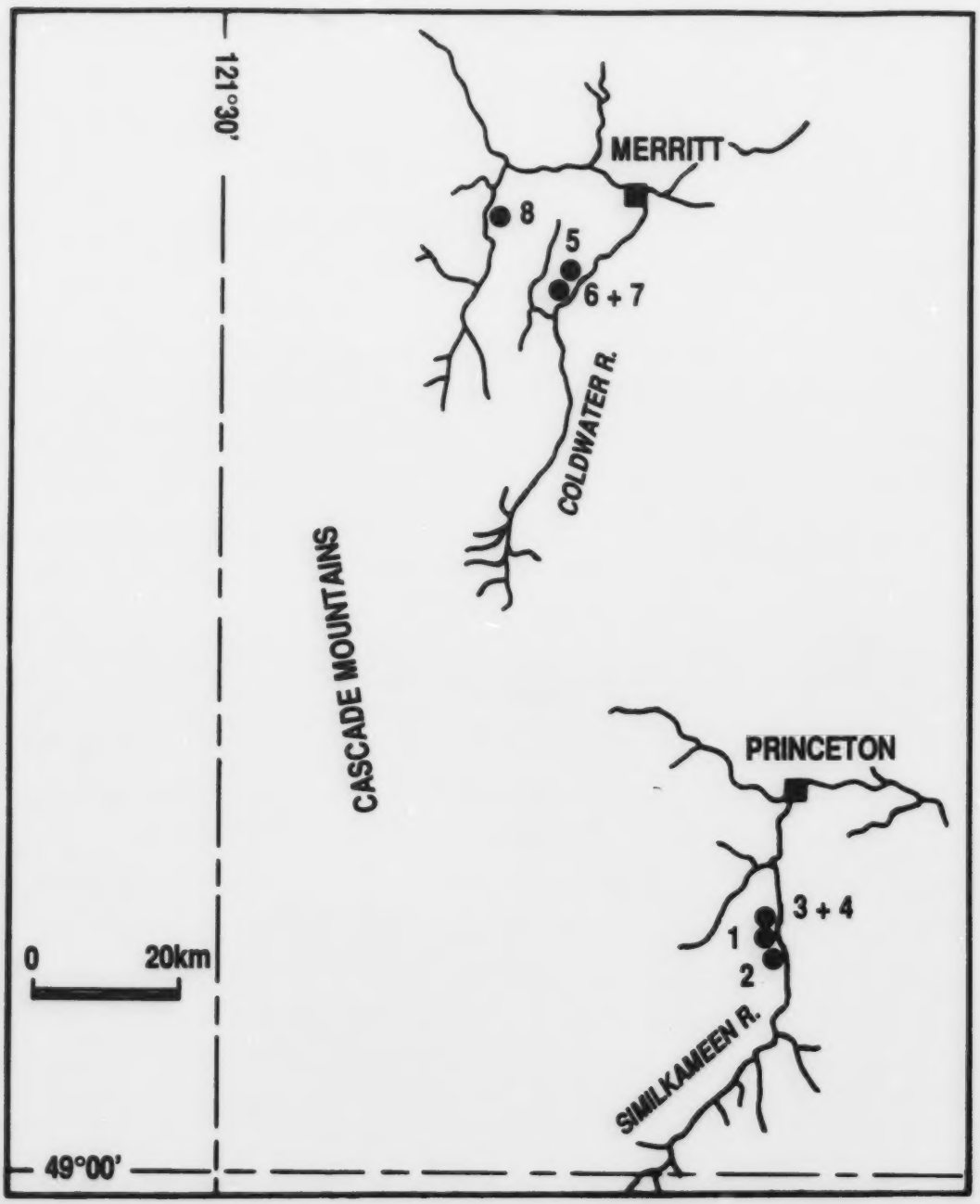

Figure 1. Approximate locations of the Princeton and Merritt study areas.

Site 2 was heavily cut; all stems larger than 15cm (DSH) of the dominant tree species (Lodgepole Pine, plus lesser amounts of Englemann Spruce and Subalpine Fir (*Abies lasiocarpa*)) were removed. The relatively few Douglas-fir were left standing.

Site 3 was originally designated as the uncut control forest, and was surveyed in 1983 and 1984. However, during the summer of 1985, this stand was cut, precluding any surveys that year. Timber was extracted with a diameter limit of 35cm (DSH) for Douglas-fir and Ponderosa Pine, and 15cm for all other species (Lodgepole Pine and Engelmann Spruce). This altered stand was surveyed in 1986, and renamed site 4.

There were also three timber plots at the Merritt study area, all within 20km of Merritt. Site 5 was selectively logged during the winter of 1983/1984. Timber was removed according to a predetermined percentage of the total volume by diameter class. These percentages were: 15.2-20.3cm (diameter at breast height, DBH): 20%, 20.3-30.5cm: 25%, 30.5-61.0cm: 45% and >61.0cm: 75%. Post-cutting, the dominant forest of site 5 consisted of Douglas-fir and Ponderosa Pine, with scattered Englemann Spruce and Trembling Aspen.

Site 6 was uncut at the onset of the Merritt surveys (1984). However, during the winter of 1984/1985 it was logged to the same standards as site 5. This altered stand was renamed site 7 and was surveyed in 1985 and 1986.
Site 8, supporting primarily Ponderosa Pine and Douglas-fir, served as the uncut control for the Merritt area and remained intact for the duration of the study. This site was contained within a proposed B.C. Ecological Reserve (Jack Swart Creek Reserve, ERP #305).

For a more detailed description of each site (location, size, elevation and slope) see Morgan *et al.*(1989).

3. METHODS.

3.1. Field Methods.

3.1.1. Monitoring of bird foraging behaviour.

Most observations on the foraging behaviour of forest birds were made between 05:30 and 12:00. Usually, two observers wandered throughout the site searching for foraging birds. We attempted to cover most of the study area each survey day. Observations were made on eleven species of birds, although not all species occurred on all sites. The species observed were: Red-naped Sapsucker (*Sphyrapicus nuchalis*), Mountain Chickadee (*Parus gambeli*), Red-breasted Nuthatch (*Sitta canadensis*), White-breasted Nuthatch (*S.carolinensis*), Golden-crowned Kinglet (*Regulus satrapa*), Yellow-rumped Warbler (*Dendroica coronata*), Townsend's Warbler (*D.townsendi*), Chipping Sparrow (*Spizella passerina*), Cassin's Finch (*Carpodacus cassinii*) and Western Tanager (*Piranga ludoviciana*). Two species of flycatcher, Hammond's (*Empidonax hammondii*) and Dusky (*E.oberholseri*) could not be consistently identified throughout this study. Others, such as Beedy (1981) and Mannan (1982) have experienced the same difficulty. While we recorded foraging observations on this pair complex, we will simply refer to them as *Empidonax* species.

Immature birds often feed less efficiently than adults (McKean 1990). Due to inexperience and/or their subordinate status, the immature birds frequently forage in a different manner, at a different location or for different prey. Consequently, we recorded the foraging behaviour of adults only.

After a foraging bird was encountered, instantaneous observations were made every fifteen seconds. Consecutive observations of foraging behaviour are time-dependent, and therefore violate the assumptions of independence when testing for significance (Balda 1969). However, Landres and MacMahon (1980) and Mannan (1982) believed that for birds that were actively pursuing prey in trees, the fifteen second interval was adequate to insure independence. Mannan (1982) tested this assumption, by randomly selecting one observation from each set of observations, and comparing the results with the full complement of data. The two methods produce virtually identical results. For further discussions pertaining to

sequential vs. initial observations, see Hejl et al. (1990), Recher and Gebski (1990), Brennan and Morrison (1990) and Petit *et al.* (1990).

Due to potential problems associated with consecutive observations, we limited our observations to a maximum of twelve for any one bird on a given day. Over the course of the study, large sample sizes were achieved for most species, hopefully further reducing the observation problems. The foraging observations that we made, closely followed those described by Franzreb (1983b). The eight classes of foraging observations were:

1) foraging method (eg gleaning, pecking etc.);
2) activity surface (eg trunk, branch, foliage);
3) diameter of the perch where the activity was taking place;
4) horizontal location (eg near branch tip, near trunk);
5) activity height;
6) tree (or shrub) species;
7) tree (or shrub) height;
8) stem diameter of the tree (or shrub).

Four of the variables (perch diameter, tree height, stem diameter and activity height) were recorded by relatively broad class intervals.

3.1.2. Measurement of vegetation.

Within each site, the vegetation was sampled at twenty points evenly spaced throughout the stand, in a manner similar to Mannan (1982). Within a 0.07ha circular plot, all trees (>2.5cm, DBH) were counted, identified, and placed in height and diameter classes. In addition, canopy volume, cover by height categories, ground cover and percent slash cover were also estimated. For a more detailed description of these methods, see Morgan *et al.*(1989).

3.2.Data Analysis.

3.2.1.Determining Foraging Behaviour and Comparing Habitat Use with Availability.

The initial stage of the analysis involved calculating the percentage of the total observed movements within each of the eight foraging classes by

foraging categories. This resulted in a total of thirty-seven categories. In this part of the analysis, we combined the data from all sites and years. Determining the proportion of the total movements (e.g. 73% pecking, 26% gleaning and 1% hawking) produces an average "preferred" method, surface etc. As some activities such as hawking, or ground foraging removed the bird from a tree surface, the total number of movements varied between certain foraging classes.

The next step in the analysis compared the use of quantifiable variables (ie. number stems/ha by: tree species, tree heights, stem diameters) with availability. To do this we calculated an index of habitat utilization (Jacobs 1974) for each species of bird on each site as follows:

$$D_{hb} = \frac{r-p}{r+p-2rp}$$

where D_{hb} is the index of habitat utilization, r is the proportional use of a given variable, and p is the proportional availability of that variable (Morrison 1981). D_{hb} varies from -1.00 to +1.00, with negative values indicating under-utilization compared with availability, while positive values indicate over-utilization. Morrison (1981) used the following criteria: a D_{hb} of 0 to ± 0.15 implied no preference; ± 0.16 to 0.40, slight avoidance or preference; ± 0.41 to 0.80, moderate avoidance or preference; and ± 0.81 to 1.00 strong avoidance or preference.

The Log-likelihood Ratio (G statistic, Zar 1984) was used to test for significant differences between trees species use and availability. This was calculated for each species by site, as well as all sites combined. The same method was used to compare tree height and stem diameter utilization with availability.

3.2.2. Niche Overlap and Potential Competition.

The thirty-seven foraging category proportions (non-transformed) were used to run an unweighted, Average-linkage Cluster Analysis (based on the Pearson Product-moment Correlations between bird species). The resultant dendrogram graphically demonstrated the foraging behaviour relationships between species.

To further examine the degree of foraging similarity between species, we calculated niche overlap (Schoener 1968) as follows:

$$O_{xy}=1-\frac{1}{2}\Sigma|P_{x_i}-P_{y_i}|$$

where P_{x_i} is the proportion of time spent in resource state i by species x. Niche Overlap represents the amount of overlap between two species (x and y), with total overlap along a given dimension producing a value of 1.00. In this analysis, we calculated the degree of overlap for each of the eight foraging classes, and then determined the mean overlap (of the eight classes) between all bird species-pair combinations. *Empidonax* species foraging data were not included in this analysis because of the aforementioned identification problems.

According to Cody (1974) similar-sized species tend to forage similarly, and within a foraging guild, there is a positive correlation between body size and average prey size (Hespenheide 1971, in Virkkala 1988). In a manner similar to Virkkala (1988), we examined the relationships between species-pair weight ratios and species-pair niche overlap of arboreal foragers. The weights used in the analysis were as follows: Red-naped Sapsucker 50.7g, Western Tanager 27.3g, White-breasted Nuthatch 17.2g, Mountain Chickadee 12.3g, Yellow-rumped Warbler 11.9g, Townsend's Warbler 11.3g, Red-breasted Nuthatch 10.2g and Golden-crowned Kinglet 6.0g (Beedy 1981). Cassin's Finch and Chipping Sparrow were excluded from this analysis, as these species forage predominantly on the ground.

3.2.3. Foraging Variability Between Sites and Years.

We calculated the niche overlap between the ten bird species-pair combinations from four subsets of the data. These subsets were: uncut (and lightly cut) sites (no. 1,3,4,5,6,8); heavily cut (no. 2,7); the Princeton sites (no. 1-4); and the Merritt sites (no. 5-8). In order to examine the effects of habitat alteration on foraging behaviour we applied the Wilcoxon Paired-sample Test (Zar 1984) comparing the degree of species-pair overlap between: a) uncut/lightly cut and heavily cut stands; and b) Princeton and Merritt sites.

In order to evaluate the effects of combining data from different years and different areas, the proportions of each foraging variable from each site were subjected to a multiple analysis of variance. Hotellings test (Zar 1984) was used to identify significant intra-year and intra-site differences. Only those sites with three or more years of data (no. 1,2,5,8) were used in this analysis.

4. RESULTS and DISCUSSION.

4.1. Foraging Behaviour and Habitat Use.

In appendix 1, we list population densities (of the species covered in this report), bird species diversities, species richness and foraging guild densities for each site year by year; in appendix 2, we present the vegetation characteristics of each site. For a detailed examination of the relationships that were observed between population variables and habitat characteristics, see Morgan *et al.* (1989).

The types of foraging method, locations, tree species and tree sizes that were most frequently used, varied between and within species (Table 1). However, at least in broad terms, each species' foraging behaviour was definable. To group species with similar foraging methods into guilds, we assigned the eleven bird species studied into the following foraging associations:

1) **Pecking/Probing** - Red-naped Sapsucker;

2) **Hawking/Flycatching** - the 2 *Empidonax* flycatchers;

3) **Gleaning** - the remaining 9 species. Gleaners were further divided into:

   i) **Foliage Gleaners** - Mountain Chickadee, Golden-crowned Kinglet, Yellow-rumped Warbler, Townsend's Warbler, and Western Tanager;

   ii) **Branch/Trunk Gleaners** - Red-breasted and White-breasted nuthatches;

   iii) **Ground Gleaners** - Chipping Sparrow and Cassin's Finch.

Table 1. Summary of foraging variables for 11 species of birds. Data listed are the total number of observed movements and the percentages (of the total) by foraging variable. Data from all years and sites have been combined. The highest percentage in each of the variable categories is highlighted by an asterisk.

Foraging variables (% of total movements)	BIRD SPECIES										
	RNSA	EMPI	MOCH	RBNU	WBNU	GCKI	YRWA	TOWA	CHSP	CAFI	WETA
Foraging Activity	n=923	n=207	n=2213	n=1206	n=485	n=81	n=1722	n=431	n=874	n=331	n=162
Glean	26.1	25.1	*85.9	*71.6	*61.9	*65.4	*83.4	*94.9	*96.3	*96.4	*93.2
Hover	0.0	4.8	0.9	0.6	0.4	32.1	10.5	4.4	1.7	1.2	3.1
Hawk	1.0	*69.6	0.2	0.8	0.0	0.0	3.8	0.2	1.6	0.3	3.7
Peck/Probe	*72.9	0.5	13.0	27.0	37.7	2.5	2.3	0.5	0.4	2.1	0.0
Activity Surface	n=923	n=207	n=2213	n=1206	n=485	n=81	n=1722	n=431	n=874	n=331	n=162
Trunk	*85.5	1.5	2.0	32.3	*62.5	0.0	2.7	0.5	1.0	0.6	1.2
Branch/Twig	7.5	30.9	24.1	*33.7	31.1	24.7	25.2	12.7	4.0	14.5	10.5
Foliage	4.5	*36.2	*58.2	26.2	2.5	*60.5	*64.2	*85.8	28.3	20.2	*88.3
Cone	0.1	0.0	12.1	5.2	0.0	14.8	4.4	0.5	0.7	17.2	0.0
Ground	0.0	2.4	2.2	0.1	0.4	0.0	1.8	0.0	*41.2	*23.9	0.0
Log/Slash	1.2	16.4	0.7	0.7	1.2	0.0	1.0	0.0	4.3	0.6	0.0
Snag	0.9	2.0	0.5	1.8	2.3	0.0	0.1	0.0	0.0	0.0	0.0
Herb/Grass	0.0	10.6	0.2	0.0	0.0	0.0	0.6	0.5	20.5	23.0	0.0
Perch Diameter	n=911	n=144	n=2144	n=1190	n=477	n=81	n=1663	n=429	n=303	n=174	n=162
<2.5cm	5.2	*97.9	*89.9	*44.6	6.3	*98.8	*93.0	*99.6	*98.0	*95.4	*96.9
2.5 - 5.0	5.2	0.7	7.4	11.5	10.9	1.2	4.6	0.2	1.4	4.0	1.9
5.0 - 10.0	11.9	1.4	1.8	7.8	10.9	0.0	1.2	0.2	0.3	0.0	0.0
>10.0	*77.7	0.0	0.9	36.1	*71.9	0.0	1.2	0.0	0.3	0.6	1.2
Horizontal Location	n=911	n=144	n=2144	n=1190	n=477	n=81	n=1663	n=429	n=303	n=174	n=162
Near branch tip	2.9	*55.5	*60.3	32.5	6.1	*53.1	*61.7	*56.4	*76.9	*56.9	*43.8
Mid-branch	4.8	29.2	29.5	21.6	16.4	39.5	29.0	35.4	21.1	34.5	40.7
Near trunk	*92.3	15.3	10.2	*45.9	*77.5	7.4	9.3	8.2	2.0	8.6	15.5
Vertical Location	n=912	n=145	n=2144	n=1190	n=481	n=81	n=1663	n=429	n=296	n=174	n=162
0.0 - 1.3m	15.8	7.6	3.1	5.4	9.9	0.0	4.2	1.2	8.1	6.9	1.9
>1.3 - 5.0	*36.6	*33.8	17.9	19.5	15.4	21.0	17.8	15.2	30.4	8.0	*32.1
>5.0 - 10.0	29.1	22.1	29.5	32.1	25.6	*43.2	34.6	20.7	*41.9	*55.8	29.6
>10.0 - 20.0	17.0	26.9	*40.9	*36.2	*41.4	33.3	*38.1	*53.6	18.2	27.6	25.3
>20.0 - 30.0	1.3	9.6	8.0	6.2	7.7	2.5	5.0	9.3	1.4	1.7	10.5
>30.0	0.2	0.0	0.6	0.6	0.0	0.0	0.3	0.0	0.0	0.0	0.6
Tree Species	n=920	n=158	n=2178	n=1198	n=479	n=81	n=1664	n=429	n=387	n=192	n=162
Ponderosa Pine	2.5	17.1	21.5	31.8	*63.9	0.0	17.6	0.0	15.5	14.6	7.4
Douglas-fir	*64.6	*63.3	*70.8	*62.3	32.8	*86.4	*72.8	*75.1	*75.9	*78.6	*88.9
Trembling Aspen	19.9	2.5	0.6	1.3	1.0	0.0	0.5	1.6	0.3	0.0	0.0
Other trees (alive)	12.2	14.6	6.6	2.8	0.0	13.6	9.1	23.3	8.3	6.8	3.7
Snags	0.8	2.5	0.5	1.8	2.3	0.0	0.0	0.0	0.0	0.0	0.0
Trunk Diameter (dbh)	n=912	n=154	n=2171	n=1776	n=469	n=81	n=1665	n=429	n=377	n=192	n=162
<10cm	6.7	12.3	6.7	3.0	0.0	3.7	8.6	7.7	17.5	2.6	4.9
>10.0 - 20.0	30.2	11.0	18.7	12.7	5.3	17.3	18.4	19.6	18.8	15.4	15.4
>20.0 - 40.0	*47.9	35.7	36.6	35.0	19.4	*66.7	*39.9	*37.8	*36.1	*46.7	*52.5
>40.0	15.2	*41.0	*38.0	*49.3	*75.3	12.3	33.1	34.9	27.6	35.3	27.2
Tree Height	n=912	n=154	n=2171	n=1176	n=469	n=81	n=1665	n=429	n=377	n=192	n=162
<10.0m	20.0	19.5	17.7	13.3	8.1	13.6	18.4	14.0	34.5	8.3	18.5
10.0 - 20.0	*56.6	37.0	*50.8	*43.7	37.7	*55.5	*46.7	33.6	*49.6	39.6	*46.3
>20.0	23.4	*43.5	31.5	43.0	*54.2	30.9	34.9	*52.4	15.9	*52.1	35.2

Note: species abbrevations are as follows: RNSA = Red-naped Sapsucker, EMPI = Epidonax sp., MOCH = Mountain Chickadee, RBNU = Red-breasted Nuthatch, WBNU = White-breasted Nuthatch, GCKI = Golden-crowned Kinglet, YRWA = Yellow-rumped Warbler, TOWA = Townsend's Warbler, CHSP = Chipping Sparrow, CAFI = Cassin's Finch, WETA = Western Tanager.

There was no consistent trend in the habitat utilization indices for each bird species (Table 2). This was likely in part, an artefact created by grouping data from different sites and years. However, it probably also demonstrated the foraging plasticity of the species as they reacted to an unknown number of environmental conditions. In spite of this "blurring" of the data, a few generalities were discernible: Red-naped Sapsuckers and White-breasted Nuthatches generally avoided Douglas-fir; Western Tanagers and Cassin's Finches (when not ground foraging) tended to strongly select Douglas-fir; other than Red-naped Sapsucker, all species moderately to strongly avoided Trembling Aspens; Ponderosa Pines were generally under-utilized other than by White-breasted Nuthatches (in the Merritt sites); and most species moderately to completely avoided foraging in snags (Table 2). The avoidance of Aspen by most species may have related to its leaf morphology and size. The large leaf size makes it difficult for birds to perch on a branch and reach the middle and outer portions of a leaf, that may harbour insects; while species that hover may find it difficult to detect and capture prey because the Aspen leaf flutters in even the slightest breeze (Franzreb 1978, Jackson 1979). The general avoidance of Ponderosa Pine may also have been related to suboptimal foraging: it may be extremely difficult to detect prey at the base of the long (12-20cm) needle clusters. Compounding this, it may also be extremely hard to locate a perch that will not only support a bird's weight, but will also place it close enough to reach the centre of the needle cluster.

In the comparisons between tree height category availability and use, trends were somewhat more obvious (Table 3). All species avoided (slightly to strongly) tree less than 10m in height. In contrast, trees in the height classes 10-20m, and >20m were moderately to strongly favoured. Franzreb (1983a) similarly noted that birds preferred to forage in moderately to tall trees. She believed that taller trees not only provided greater numbers of foraging substrates, but also contained more foliage than smaller trees. More foliage and substrates may

Table 2. Habitat utilization indices comparing bird species use of tree species, with tree species proportional availability. Data from all years have been combined. Values range from -1.00 (total avoidance) to +1.00 (absolute preference). Absence of foraging observations is indicated by N. Fewer than 10 foraging movements were considered insufficient for analysis, and are indicated by I. See Table 1 for bird species abbreviations.

A) Douglas-fir

	Site Number							
Bird Species	1	2	3	4	5	6	7	8
RNSA	-0.42	0.81	N	-0.08	-0.80	I	0.04	I
EMPI	-0.13	0.80	N	N	-0.19	N	0.38	0.06
MOCH	-0.31	0.89	-0.44	0.37	-0.09	0.73	0.63	0.37
RBNU	-0.15	0.79	0.44	0.90	-0.32	-0.29	0.38	0.01
WBNU	N	I	N	N	-0.24	-1.00	-0.95	-0.44
GCKI	-0.23	N	0.38	1.00	N	N	N	I
YRWA	-0.11	0.88	0.29	0.89	-0.49	0.24	0.62	0.24
TOWA	-0.48	0.79	0.17	0.57	I	I	I	I
CHSP	-0.49	0.74	I	1.00	0.38	0.49	0.78	0.43
CAFI	1.00	0.96	I	N	0.13	I	0.77	0.60
WETA	1.00	I	N	1.00	0.41	N	I	0.65

B) Trembling Aspen

	Site Number							
	1	2	3	4	5	6	7	8
	0.14	0.42	N	0.94	0.48	I	0.81	I
	-1.00	-0.33	N	N	-1.00	N	-1.00	-1.00
	-1.00	-0.57	-1.00	0.71	-1.00	-1.00	-0.85	-1.00
	-0.13	0.01	-1.00	-1.00	-0.27	-1.00	-1.00	-1.00
	N	I	N	N	-1.00	-1.00	0.25	-1.00
	-1.00	N	-1.00	-1.00	N	N	N	I
	-1.00	-0.68	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
	0.37	-1.00	-1.00	-1.00	I	I	I	I
	-1.00	-0.54	I	-1.00	-1.00	-1.00	-1.00	-1.00
	-1.00	-1.00	I	N	-1.00	I	-1.00	-1.00
	-1.00	I	N	-1.00	-1.00	N	I	-1.00

C) Ponderosa Pine

	Site Number							
Bird Species	1	2	3	4	5	6	7	8
RNSA	-1.00	-1.00	N	-1.00	-0.45	I	-0.87	I
EMPI	0.89	-1.00	N	N	0.13	N	-0.73	0.04
MOCH	0.82	-1.00	-1.00	-1.00	0.15	-0.69	-0.55	-0.32
RBNU	0.91	-1.00	-1.00	-1.00	0.36	0.40	-0.22	0.03
WBNU	N	I	N	N	0.31	1.00	0.80	0.43
GCKI	-1.00	N	-1.00	-1.00	N	N	N	I
YRWA	0.79	-1.00	-1.00	-1.00	0.08	-0.11	-0.58	-0.23
TOWA	-1.00	-1.00	-1.00	-1.00	I	I	I	I
CHSP	-1.00	0.93	I	-1.00	-0.55	-0.33	-0.75	-0.43
CAFI	-1.00	-1.00	I	N	-0.25	I	-0.69	-0.41
WETA	-1.00	I	N	-1.00	-0.59	N	I	-0.59

D) Snags

	Site Number							
	1	2	3	4	5	6	7	8
	-0.18	-0.76	N	0.36	-1.00	I	-0.24	I
	-1.00	0.12	N	N	0.66	N	0.46	-1.00
	-0.24	-0.55	-1.00	-1.00	-1.00	-0.14	-1.00	-0.65
	-0.32	0.64	-0.04	-1.00	-0.11	0.27	-1.00	0.17
	N	I	N	N	-1.00	-1.00	-1.00	0.35
	-1.00	N	-1.00	-1.00	N	N	N	I
	-1.00	-0.81	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
	-1.00	-1.00	-1.00	-1.00	I	I	I	I
	-1.00	-1.00	I	-1.00	-1.00	-1.00	-1.00	-1.00
	-1.00	-1.00	I	N	-1.00	I	-1.00	-1.00
	-1.00	I	N	-1.00	-1.00	N	I	-1.00

result in more prey (types, abundance and distribution) (Manuwal 1983), as well as greater shelter from inclement weather and escape cover from predators.

Balda's (1967) observations of the early morning sun warming the upper parts of the canopy first, and the resultant increased insect activity, leads to an alternate explanation. We suggest that in general, the tallest trees receive the earliest morning sunlight, and consequently are the first areas with significant arthropod activity. Those trees would likely be the first areas an arboreal forager would visit. In addition, as Franzreb (1983a) noted, most foraging observations are taken in the early morning, which probably biases the result in favour of tall trees and upper canopy foraging.

Small (<10cm) and medium (<20cm) trunk diameter trees were strongly to weakly avoided, whereas moderate (<40cm) and large (>40cm) diameter trees were highly favoured (Table 4). It is unlikely that arboreal foragers were selecting for large stems; their choosing of a tree was most likely based on either foliage characteristics, height preferences, or food distribution patterns. On the other hand, trunk gleaners and probers may have been selecting the trees solely on the basis of large stems and the associated arthropods on and beneath the bark. Jackson (1979) noted that variability in bark roughness within and among tree species influenced the abundance of surface arthropods and their detectability by birds.

With few exceptions, use of the forest by the eleven bird species differed significantly from what was available on each site (Table 5). When the data from all sites and years are combined, every bird species with the exception of the flycatchers, utilize the forests (in terms of tree species, height and trunk availability) in significantly different proportions than they would if they were foraging randomly throughout the stands (ie. not partitioning the resources).

Table 3. Habitat utilization indices comparing bird species use of trees by height category, with tree height proportional availability. Data from all years have been combined. Values range from −1.00 (total avoidance) to +1.00 (absolute preference). No foraging observations indicated by N. Insufficient observations indicated by I. See Table 1 for bird species abbreviations

A) Trees < 10.0m in Height

	Site Number							
Bird Species	1	2	3	4	5	6	7	8
RNSA	−0.84	−0.91	N	−0.91	−0.66	I	−0.82	I
EMPI	−0.68	−0.86	N	N	−0.87	N	−0.89	−0.92
MOCH	−0.79	−0.94	−0.78	−0.88	−0.82	−0.75	−0.88	−0.68
RBNU	−0.89	−0.93	−0.98	−0.88	−0.82	−0.84	−0.86	−0.99
WBNU	N	I	N	N	−0.88	−1.00	−0.91	−0.96
GCKI	−0.82	N	−1.00	−0.45	N	N	N	I
YRWA	−0.89	−0.91	−0.85	−0.93	−0.83	−0.85	−0.69	−0.87
TOWA	−0.78	−0.96	−0.98	−0.73	I	I	I	I
CHSP	−0.33	−0.84	I	−0.80	−0.69	−0.89	−0.52	−0.55
CAFI	−1.00	−0.96	I	N	−0.98	I	−0.83	−0.93
WETA	−0.72	I	N	−0.73	−0.90	N	I	−0.94

B) Trees 10.0 – 20.0m in Height

	Site Number							
	1	2	3	4	5	6	7	8
	0.49	0.82	N	0.30	0.57	I	0.77	I
	0.67	0.43	N	N	−0.03	N	0.76	−0.02
	0.48	0.66	0.67	−0.02	0.51	0.41	0.69	0.44
	0.57	−0.19	0.29	0.40	0.45	0.27	0.39	0.35
	N	I	N	N	0.01	−0.05	0.78	0.26
	0.86	N	0.55	0.18	N	N	N	I
	0.66	0.56	0.64	0.30	0.49	0.44	0.29	0.44
	−0.12	0.27	0.39	0.47	I	I	I	I
	0.45	0.52	I	0.26	0.41	0.83	0.42	0.46
	0.03	0.36	I	N	0.32	I	0.53	0.24
	0.58	I	N	−0.42	0.63	N	I	−0.59

C) Trees > 20.0m in Height

	Site Number							
Bird Species	1	2	3	4	5	6	7	8
RNSA	0.77	0.69	N	0.88	0.59	I	0.55	I
EMPI	0.07	0.89	N	N	0.96	I	0.79	0.92
MOCH	0.72	0.88	0.46	0.92	0.87	0.87	0.86	0.73
RBNU	0.76	0.97	0.91	0.84	0.89	0.93	0.94	0.87
WBNU	N	I	N	N	0.96	0.98	0.80	0.89
GCKI	−1.00	N	0.85	0.62	N	N	N	I
YRWA	0.67	0.89	0.65	0.89	0.88	0.90	0.89	0.78
TOWA	0.91	0.96	0.89	0.68	I	I	I	I
CHSP	−1.00	0.85	I	0.85	0.83	0.51	0.62	0.36
CAFI	0.94	0.95	I	N	0.96	I	0.89	0.87
WETA	0.51	I	N	0.92	0.87	N	I	0.98

Table 4. Habitat utilization indices comparing bird species use of trees by trunk diameter category (measured at breast height), with trunk diameter proportional availability. Data from all years have been combined. Values range from −1.00 (total avoidance) to +1.00 (absolute preference). No foraging observations indicated by N. Insufficient observations indicated by I. See Table 1 for bird species abbreviations.

A) Tree Stems ≤ 10.0cm (dbh)

Bird Species	Site Number 1	2	3	4	5	6	7	8
RNSA	−0.96	−0.94	N	−0.91	−0.91	I	−0.92	I
EMPI	−0.92	−0.86	N	N	−0.78	I	−0.82	−1.00
MOCH	−0.96	−0.93	−0.74	−0.91	−0.87	−0.87	−0.93	−0.88
RBNU	−0.99	−1.00	−1.00	−0.93	−0.88	−0.96	−0.94	−1.00
WBNU	N	I	N	N	−1.00	−1.00	−1.00	−1.00
GCKI	−0.82	N	−1.00	−1.00	N	N	N	I
YRWA	−0.91	−0.89	−0.93	−0.97	−0.90	−0.85	−0.81	−0.87
TOWA	−0.92	−0.98	−0.99	−0.81	I	I	I	I
CHSP	−0.64	−0.87	I	−1.00	−0.78	−1.00	−0.55	−0.61
CAFI	−1.00	−1.00	I	N	−1.00	I	−0.83	−1.00
WETA	−0.97	I	N	−0.93	−0.81	I	I	−0.91

B) Tree Stems 10.0 − 20.0cm (dbh)

Site Number 1	2	3	4	5	6	7	8
0.16	0.25	N	−0.09	0.27	I	0.37	I
−1.00	0.11	N	N	−0.79	I	−0.57	−0.59
0.38	0.01	0.31	−0.03	−0.41	−0.10	−0.45	−0.40
−0.16	−0.06	−0.43	−0.09	−0.62	−0.81	−0.47	−0.32
N	I	N	N	−0.69	−1.00	−0.49	−0.86
−1.00	N	−0.34	0.58	N	N	N	I
−0.24	0.05	0.01	−0.25	−0.22	−0.77	−0.03	−0.48
−0.05	0.18	−0.36	−0.03	I	I	I	I
−0.04	0.16	I	−0.18	−0.56	−1.00	−0.08	0.20
−0.09	−1.00	I	N	−0.02	I	−0.33	−1.00
0.06	I	N	−0.18	−0.88	I	I	−1.00

C) Tree Stems 20.1 − 40.0cm (dbh)

Bird Species	Site Number 1	2	3	4	5	6	7	8
RNSA	0.82	0.89	N	0.83	0.53	I	0.60	I
EMPI	0.96	0.75	N	N	0.15	I	0.83	−0.02
MOCH	0.75	0.83	0.71	0.73	0.49	0.23	0.69	0.55
RBNU	0.73	0.69	0.71	0.81	0.62	0.50	0.45	0.25
WBNU	N	I	N	N	0.04	−1.00	0.71	0.15
GCKI	0.95	N	0.94	0.44	N	N	N	I
YRWA	0.83	0.84	0.60	0.79	0.68	0.06	0.48	0.64
TOWA	0.72	0.59	0.58	0.78	I	I	I	I
CHSP	0.83	−0.15	I	0.69	0.78	0.87	0.20	0.18
CAFI	0.80	0.23	I	N	0.62	I	0.62	0.85
WETA	0.88	I	N	0.75	0.77	I	I	−0.04

D) Tree Stems > 40.0cm (dbh)

Site Number 1	2	3	4	5	6	7	8
0.89	0.71	N	0.89	0.78	I	0.56	I
0.84	0.87	N	N	0.97	I	0.75	0.93
0.86	0.88	−1.00	0.94	0.93	0.86	0.90	0.72
0.98	0.96	0.92	0.89	0.93	0.92	0.95	0.86
N	I	N	N	0.98	1.00	0.92	0.93
−1.00	N	0.58	0.79	N	N	N	I
0.94	0.83	0.89	0.94	0.86	0.95	0.86	0.66
0.96	0.95	0.98	0.81	I	I	I	I
−1.00	0.95	I	0.96	0.81	0.74	0.87	0.51
0.96	0.99	I	N	0.88	I	0.89	0.56
0.74	I	N	0.98	0.86	I	I	0.95

4.1.1. Summaries of Foraging Behaviour by Species.

This section summarizes on a species basis, the results of Tables 1-5, and compares our results with that of others. The reader is reminded that in light of the high degree of variability previously described (section 1.1.), the following descriptions depict the 'average' foraging behaviour of each species, which may only be representative of the locations and conditions in which they were studied.

Red-naped Sapsucker.

Red-naped Sapsuckers preferred to forage by pecking/probing the trunks of trees 10-20m in height, with stem diameters greater than 20cm. Most foraging events took place between 1.3 and 5m above the ground. Although most foraging occurred on Douglas-firs, sapsuckers actually under-utilized this species as well as Ponderosa Pines and snags, compared with their availabilities. In contrast, Trembling Aspen were used more frequently than expected. In Arizona, Franzreb (1977) found that Yellow-bellied Sapsuckers (Sphyrapicus varius, conspecific with *S.nuchalis* pre-1983, AOU 1983) foraged primarily on Engelmann Spruce, Trembling Aspen and snags in an unlogged area, while showing a preference for Subalpine Fir, White Fir (*Abies concolor*), Douglas-fir and snags on a cut site. However, in both areas, aspen was under-utilized. In Franzreb's study, trees taller than 21m were apparently selected.

Mountain Chickadee.

Mountain Chickadees foraged predominantly by foliage gleaning, near the distal ends of branches, usually 10-20m above the ground. The majority of foraging occurred on thick trunked, tall trees. Douglas-firs were over-utilized, whereas Aspen, Ponderosa Pine and snags were under-exploited, compared to their abundance. Franzreb (1977) found that Mountain Chickadees in Arizona favoured Douglas-fir, White Fir, Blue Spruce (*Picea pungens*) and Engelmann Spruce on an

Table 5. Summary of G-test results comparing bird species use of habitat variables (tree species, tree heights, trunk diameters) with availability. Data were analyzed by site (all years combined) and overall (all sites and years combined). Significance levels as follows: *** = p<0.001 ** = p<0.005, * = p<0.01, ns = no significant differences between use and availability. No foraging observations indicated by N. Insufficient observations indicated by I.

	Site Number								
	1	2	3	4	5	6	7	8	Overall
Red-naped Sapsucker									
Tree Species Abundance	*	***	N	***	***	I	***	I	***
Tree Heights	***	***	N	***	***	I	***	I	***
Trunk Diameters	***	***	N	***	***	I	***	I	***
Empidonax Sp.									
Tree Species Abundance	ns	***	N	N	ns	N	***	ns	ns
Tree Heights	ns	***	N	N	***	N	***	***	***
Trunk Diameters	***	***	N	N	***	N	***	***	***
Mountain Chickadee									
Tree Species Abundance	***	***	*	***	***	***	***	***	***
Tree Heights	***	***	***	***	***	***	***	***	***
Trunk Diameters	***	***	***	***	***	***	***	***	***
Red-breasted Nuthatch									
Tree Species Abundance	***	***	ns	***	***	***	***	ns	***
Tree Heights	***	***	***	***	***	***	***	***	***
Trunk Diameters	***	***	***	***	***	***	***	***	***
White-breasted Nuthatch									
Tree Species Abundance	N	I	N	N	***	***	***	***	***
Tree Heights	N	I	N	N	***	***	***	***	***
Trunk Diameters	N	I	N	N	***	***	***	***	***
Golden-crowned Kinglet									
Tree Species Abundance	ns	N	ns	ns	N	N	N	I	***
Tree Heights	***	N	***	ns	N	N	N	I	***
Trunk Diameters	***	N	***	***	N	N	N	I	***
Yellow-rumped Warbler									
Tree Species Abundance	***	***	ns	***	ns	***	***	***	***
Tree Heights	***	***	***	***	***	***	***	***	***
Trunk Diameters	***	***	***	***	***	***	***	***	***
Townsend's Warbler									
Tree Species Abundance	***	***	ns	***	I	I	I	I	***
Tree Heights	***	***	***	***	I	I	I	I	***
Trunk Diameters	***	***	***	***	I	I	I	I	***
Chipping Sparrow									
Tree Species Abundance	***	***	I	ns	***	ns	***	***	***
Tree Heights	*	***	I	***	***	***	***	***	***
Trunk Diameters	***	***	I	***	***	***	***	***	***
Cassin's Finch									
Tree Species Abundance	ns	***	I	N	ns	I	***	ns	***
Tree Heights	***	***	I	N	***	I	***	***	***
Trunk Diameters	***	***	I	N	***	I	***	***	***
Western Tanager									
Tree Species Abundance	*	I	N	ns	**	N	I	ns	***
Tree Heights	*	I	N	***	***	N	I	***	***
Trunk Diameters	***	I	N	***	***	N	I	***	***

uncut site, but switched to Subalpine Fir and to a lesser extent, Engelmann Spruce and Douglas-fir on a cut stand. In her logged plot, Chickadees shifted their foraging location downward and used shorter trees, thereby adapting to a shift in the vegetation structure (Franzreb 1983b). Airola and Barrett (1985) observed that Mountain Chickadees in the Sierra Nevada preferred to forage in pines, avoided White Fir, and in contrast to our results, showed no foraging height preference.

Red-breasted Nuthatch.

Red-breasted Nuthatches foraged mostly by surface gleaning small branches, especially near the trunk, as well as on trunks, and foliage. Close to 70% of all foraging took place between 5 and 20m above the ground, on the thickest, tallest trees. On average, Douglas-firs were over utilized, whereas Aspens, Ponderosa Pines and snags were avoided. Mannan (1982) found that Red-breasted Nuthatches in northeastern Oregon foraged on snags approximately 12% of the time, with the remainder split between foliage and bark surfaces. Douglas-fir was avoided, whereas other tree species were used in approximately the same proportions as their availability. Mannan also found that while in old-growth stands nuthatches foraged primarily 15-20m above the ground, in managed stands, their foraging more-or-less tracked the availability of foliage by height class.

White-breasted Nuthatch.

White-breasted Nuthatches also surface gleaned, but concentrated most of their efforts on trunks, 10-20m off the ground. The majority of foraging occurred on very large, tall trees, especially Ponderosa Pines. The apparent selection of Ponderosa Pine could have been an artefact of insufficient data from sites 1-4. However, observations from sites 5-8 demonstrated a weak to strong over-utilization of Ponderosa Pine by White-breasted Nuthatches. In Colorado, White-breasted Nuthatches in Ponderosa Pine forests foraged predominantly below 10m above the ground, with males foraging significantly lower than females. There were also significant differences in the preferred foraging locations of the

sexes: males foraged mostly on trunks, whereas females concentrated mostly on branches (McEllin 1979).

Golden-crowned Kinglet.

Golden-crowned Kinglets foraged similarly to Mountain Chickadees. However, in addition to foliage gleaning the outer tips of branches while perched, Kinglets also gleaned prey while hovering. Kinglets and Yellow-rumped Warblers were the only species that frequently used hovering as a foraging method. The majority of feeding activities occurred between 5 and 10m off the ground, placing Kinglets beneath many potential competitors. There were insufficient observations to make conclusive comments about the types of tree preferred for foraging, but it appeared that Douglas-firs were selected, whereas Aspen, Ponderosa Pine and snags were avoided. In Colorado (Mannan 1982) found that in old-growth stands, Golden-crowned Kinglets strongly favoured foraging in Grand Firs (*Abies grandis*) especially between 5 and 20m above the ground. Engelmann Spruce, Douglas-fir and Blue Spruce were the preferred tree species in Arizona, whereas pines and snags were avoided (Franzreb 1984). Both Manuwal (1983) and Franzreb (1984) suggested that there was a preference for areas of thick, dense canopy; possibly reflecting areas of high needle (and prey?) density.

Yellow-rumped Warbler.

Yellow-rumped Warblers also foraged like Mountain Chickadees. The majority of the manoeuvres were foliage gleaning of branch tips, primarily between 5 and 20m above the ground. As mentioned above, this warbler species frequently hovered while gleaning prey. Douglas-fir was weakly to strongly selected, whereas on average, Ponderosa Pines, Aspen and snags were under-utilized. Franzreb (1977) observed that this warbler preferred the tallest Douglas-fir, White Fir, Blue Spruce and Englemann Spruce on her uncut and cut stands in Arizona. Snags were used in approximately the same proportion as their availability, and Aspens were strongly avoided. Franzreb (1983b) considered Yellow-rumped Warblers to be quite behaviourally plastic, utilizing a wide range of vegetation types and profiles.

The ability to forage more broadly permits this species to exist in a territory smaller than many of its conspecifics (Morse 1980).

Townsend's Warbler.

Townsend's Warblers foraged similarly to Yellow-rumped Warblers; foliage gleaning branch tips. More than half of the foraging manoeuvres observed were concentrated between 10 and 20m off the ground. The limited amount of data suggested that Douglas-fir were over-utilized, while Aspen, Ponderosa Pine and snags were almost totally avoided. Additionally, the tallest trees were most highly favoured. Mannan (1982) found that this species foraged primarily in foliage 15-20m above the surface, preferring Grand Fir, while under-exploiting Douglas-fir and Ponderosa Pine. Numerous authors, including Meslow and Wight (1975) and Peterson and Peterson (1983) considered Townsend's Warbler an indicator species of mature and old-growth forests; and suggested that logging practices, especially clearcutting, severely impact upon the species. However, recent studies in coastal forests of British Columbia (Seip and Savard 1990) indicated a greater numerical abundance of Townsend's Warblers in 40-60 years old regenerating stands than in older forests. We should be cautious when generalizing about this species.

Chipping Sparrow.

The majority (>61%) of Chipping Sparrow foraging manoeuvres occurred either on the ground or in low herbs and shrubs. However, >28% of the total foraging events observed took place in trees. When feeding arboreally, they foraged primarily between 5 and 10m above the ground, gleaning branch tips. Douglas-firs were over-utilized, while Aspen, Ponderosa Pine and snags were under-exploited. This species apparently prefers open stands, for both nesting and foraging (Szaro and Balda 1986). Mannan (1982) observed that in managed stands in notheastern Oregon, Chipping Sparrows foraged on the ground or in low shrubs, approximately 60% of the time. When tree foraging, this sparrow preferred Ponderosa Pines, using other trees in either the same proportions or less than their proportional

availabilities. Mannan also observed that Chipping Sparrows generally used the lower portions of the canopy, with foliage less than 5m above the ground being over-utilized.

Cassin's Finch.

Approximately 47% of the observed foraging manoeuvres by Cassin's Finches occurred on the ground or in low growing herbs and shrubs. The majority of the remaining foraging efforts were directed towards foliage, cones, and branches. When Cassin's Finches were not ground feeding, they foraged mainly between 5 and 10m off the ground, in the largest available trees. Douglas-fir was highly over-exploited, while other trees were strongly avoided. Manuwal (1983) found that in Montana Cassin's Finch foraged primarily on the ground for seeds, especially beneath open Douglas-fir stands.

Western Tanager.

Western Tanagers foraged primarily by foliage gleaning the middle and outer portions of branches, mostly 1.3-5m above the ground. As with many other bird species, large Douglas-firs were over-utilized, while other trees were avoided. There is considerable variation in the literature concerning Western Tanager habitat preferences (foraging and breeding). Meslow and Wight (1975) and Verner (1980) believe that this species strongly favours unlogged, dense canopied stands; whereas Peterson and Peterson (1983) and Airola and Barrett (1985) claim that Western Tanager are indifferent to the effects of most logging practices. Airola and Barrett (1985) noted that close to 40% of the foraging techniques they observed were of the hawking variety. They suggested that Tanagers prefer open areas, forest edges, etc. that allow this type of foraging.

4.1.2. Niche Overlap and Potential Competition.

Cluster analyses revealed two main groupings of species in terms of their overall foraging behaviour (Fig. 2). From top to bottom, the first seven species are the gleaners. Cassin's Finch and Chipping Sparrow are primarily ground foragers, whereas Golden-crowned Kinglet, Western Tanager, Townsend's Warbler, Yellow-rumped Warbler and Mountain Chickadee are the foliage gleaners. The bottom three species (White-breasted and Red-breasted Nuthatch, and Red-naped Sapsucker) represent two foraging guilds: trunk gleaners and trunk probers. The *Empidonax* species complex appears isolated from the other species, the flycatching method of foraging contributing strongly to this isolation. In addition, combining observations of two distinct species, is likely to further exaggerate their uniqueness. If the average distance between clusters is assumed to measure the similarity of species-pairs in foraging behaviour, then the first seven species appear to be quite similar; whereas the bottom triplet have less in common.

If our measure of niche overlap reflects resource competition, Mountain Chickadees and Yellow-rumped Warblers most likely would be the strongest interspecific competitors (Table 6). High levels of competition might also be expected between (in descending order) Townsend's Warblers and Western Tanagers; Yellow-rumped and Townsend's warblers; Yellow-rumped Warblers and Western Tanagers; and Golden-crowned Kinglets and Mountain Chickadees. However, Balda (1969) suggested that closely related species can coexist in the same physical space without experiencing interspecific competition by feeding on different prey, and/or acquiring it in unique ways. This implies that in order to demonstrate the presence or absence of interspecific competition, it is necessary to identify and measure habitats on a scale finer than we used, and on many different levels. It is also necessary to show that resources are limiting (Wiens 1989).

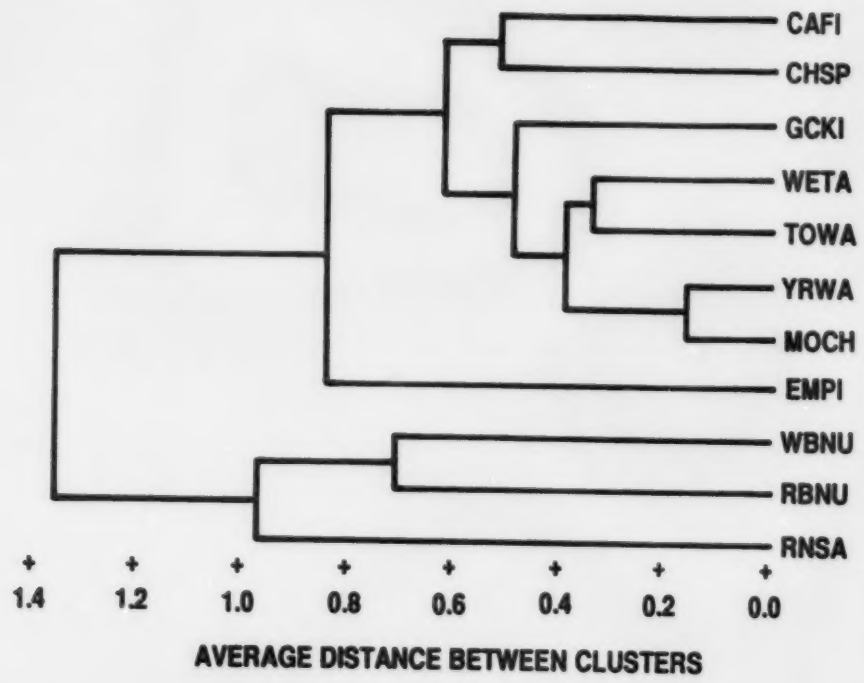

Figure 2. Cluster analysis dendrogram of bird species foraging data. See Table 1 for species abbreviations.

Table 6. Matrix of average Niche Overlap between bird species. The data for each species–pair combination represents the average niche overlap of all 8 foraging classes (e.g. method, substrate, perch diameter, etc.).

	RNSA	MOCH	RBNU	WBNU	GCKI	YRWA	TOWA	CHSP	CAFI
WETA	0.495	0.847	0.692	0.466	0.839	0.869	0.871	0.785	0.799
CAFI	0.441	0.825	0.702	0.504	0.786	0.829	0.811	0.832	
CHSP	0.474	0.761	0.646	0.419	0.756	0.811	0.754		
TOWA	0.431	0.855	0.677	0.487	0.811	0.870			
YRWA	0.487	0.942	0.755	0.524	0.858				
GCKI	0.476	0.861	0.669	0.441					
WBNU	0.665	0.553	0.758						
RBNU	0.621	0.777							
MOCH	0.498								

There was noticeably less niche overlap between the bark prober/bark gleaner guilds (Red-naped Sapsucker, White-breasted Nuthatch and Red-breasted Nuthatch, Table 6); they may have partitioned the habitat on a much coarser scale than arboreal foragers. McEllin (1979) concluded that White-breasted Nuthatches exhibited a strategy of territorial exclusivity (ie. excluding conspecifics). The generally lower niche overlap values between these three species and the remaining seven reflected the differences in foraging techniques and substrates utilized. Because of their propensity to foliage glean, Red-breasted Nuthatches overlapped noticeably more with other foliage gleaners than did the other trunk foragers.

Species most similar in weight tended to have the highest niche overlap (Table 7). We found statistically significant negative correlations between weight ratios and: (in descending order) vertical location, foraging method, horizontal location and substrate. Virkkala (1988) found highly significant correlations between weight ratios and perch diameter and horizontal location, but not vertical position. If correlation strength is a measure of how species subdivide the habitat, our results suggest that vertical location and foraging method were the most important means of partitioning the forest. Szaro and Balda (1979) found that bird species in Colorado Ponderosa Pine forests, segregated primarily on a vertical basis, or on a body weight basis; results similar to ours.

4.1.3 Foraging and Habitat Alteration

It appeared that human habitat alterations had minimal impact on the foraging behaviour of the birds we studied (Table 8). The sites were subdivided into groups: uncut/lightly cut (columns A) vs. heavily cut (columns B) in order to test for differences in niche overlap between the data groups. The splitting of the data resulted in insufficient observations for Golden-crowned Kinglet, and as before, we excluded the *Empidonax* species data. There was only one significant difference in niche overlap (Yellow-rumped Warbler/Western Tanager), although the

Table 7. Correlation results and significance levels between weight ratios and niche overlap in each of the foraging classes. Only predominantly arboreal foraging species were included in the analyses.

Dimension	Correlation	P
Foraging Method	−0.6488	0.001
Activity Substrate	−0.3764	0.05
Perch Diameter	−0.2811	ns
Horizontal Location	−0.4249	0.05
Vertical Location	−0.6741	0.001
Tree Species	0.0694	ns
Trunk Diameter	−0.0562	ns
Tree Height	−0.0230	ns
Average Overlap	−0.3993	0.05

Table 8. Comparison of niche overlap: 1) between species in uncut and lightly cut stands with those from heavily cut forests; and 2) between species in the Princeton area sites with those from the Merritt area. A = uncut/lightly cut sites (#1,3,4,5,6,8), B = heavily cut sites (#2,7); C = Princeton sites (#1–4), D = Merritt sites (#5–8). There were insufficient White-breasted Nuthatch foraging data from the Princeton sites to allow comparison with the Merritt sites. See Table 1 for bird species abbreviations.

	RNSA – RBNU				RNSA – WBNU		RBNU – WBNU		MOCH – YRWA			
Foraging Variable	A	B	C	D	A	B	A	B	A	B	C	D
Method	0.603	0.471	0.447	0.602	0.699	0.539	0.893	0.931	0.849	0.899	0.889	0.851
Substrate	0.466	0.542	0.499	0.509	0.751	0.958	0.660	0.566	0.872	0.952	0.909	0.888
Perch Diameter	0.523	0.663	0.508	0.628	0.925	0.941	0.580	0.631	0.953	0.977	0.954	0.933
Horizontal Location	0.546	0.621	0.571	0.597	0.882	0.968	0.664	0.652	0.981	0.965	0.968	0.948
Activity Height	0.765	0.769	0.712	0.639	0.729	0.819	0.933	0.739	0.868	0.903	0.912	0.928
Tree Species	0.703	0.667	0.772	0.614	0.413	0.226	0.664	0.393	0.963	0.954	0.963	0.982
Stem Diameter	0.679	0.587	0.786	0.584	0.349	0.744	0.671	0.738	0.917	0.844	0.904	0.923
Tree Height	0.878	0.706	0.813	0.676	0.711	0.917	0.833	0.700	0.944	0.820	0.962	0.930
Mean Overlap	0.645	0.628	0.639	0.606	0.682	0.764	0.737	0.669	0.918	0.914	0.933	0.923
Standard Deviation	0.137	0.094	0.148	0.049	0.204	0.261	0.130	0.155	0.049	0.058	0.032	0.039
Difference in Mean	0.017		0.033		0.082		0.068		0.004		0.010	
Significance Level	ns		ns		ns		ns		ns		ns	

	MOCH – TOWA				MOCH – WETA				YRWA – TOWA			
Foraging Variable	A	B	C	D	A	B	C	D	A	B	C	D
Method	0.841	0.960	0.925	0.846	0.835	0.889	0.829	0.846	0.887	0.863	0.901	0.874
Substrate	0.684	0.821	0.807	0.722	0.651	0.791	0.782	0.672	0.781	0.787	0.779	0.829
Perch Diameter	0.871	0.985	0.973	0.868	0.890	0.899	0.983	0.884	0.917	0.966	0.928	0.935
Horizontal Location	0.953	0.644	0.929	0.758	0.838	0.739	0.759	0.959	0.983	0.798	0.947	0.811
Activity Height	0.901	0.698	0.847	0.504	0.837	0.269	0.696	0.818	0.859	0.678	0.816	0.431
Tree Species	0.735	0.687	0.947	0.683	0.754	0.423	0.797	0.887	0.771	0.732	0.923	0.668
Stem Diameter	0.879	0.726	0.869	0.848	0.798	0.630	0.813	0.863	0.928	0.737	0.878	0.909
Tree Height	0.852	0.600	0.983	0.552	0.974	0.599	0.853	0.773	0.843	0.656	0.856	0.587
Mean Overlap	0.839	0.765	0.898	0.723	0.822	0.655	0.814	0.838	0.871	0.777	0.879	0.756
Standard Deviation	0.088	0.143	0.056	0.137	0.095	0.224	0.083	0.086	0.073	0.101	0.059	0.177
Difference in Mean	0.074		0.175		0.167		0.024		0.094		0.123	
Significance Level	ns		p<0.01		ns		ns		ns		ns	

Table 8 continued

Foraging Variable	YRWA – WETA				TOWA – WETA				CHSP – CAFI			
	A	B	C	D	A	B	C	D	A	B	C	D
Method	0.888	0.882	0.808	0.933	0.971	0.889	0.861	0.907	0.982	0.976	0.989	0.985
Substrate	0.749	0.786	0.751	0.772	0.956	0.707	0.954	0.895	0.709	0.555	0.580	0.713
Perch Diameter	0.934	0.901	0.963	0.951	0.977	0.889	0.963	0.984	0.952	0.999	0.942	0.980
Horizontal Location	0.829	0.716	0.791	0.912	0.832	0.918	0.809	0.722	0.752	0.898	0.748	0.819
Activity Height	0.826	0.280	0.706	0.802	0.739	0.208	0.585	0.529	0.336	0.364	0.324	0.367
Tree Species	0.784	0.453	0.833	0.890	0.825	0.778	0.769	0.758	0.979	0.907	0.881	0.966
Stem Diameter	0.880	0.617	0.779	0.818	0.894	0.880	0.706	0.746	0.832	0.709	0.743	0.844
Tree Height	0.940	0.725	0.869	0.808	0.878	0.863	0.735	0.779	0.572	0.741	0.578	0.682
Mean Overlap	0.854	0.670	0.812	0.861	0.884	0.766	0.798	0.790	0.764	0.769	0.723	0.795
Standard Deviation	0.069	0.214	0.078	0.068	0.084	0.236	0.128	0.141	0.226	0.222	0.222	0.209
Difference in Mean	0.184		0.049		0.118		0.008		0.005		0.072	
Significance Level	p<0.05		ns		ns		ns		ns		p<0.02	

Niche Overlap: O^{w} = (see p.11), where Pxi is the proportion of time spent in resource state i by species x (Schoener 1968). Oxy represents the extent of niche overlap between species x and y along a dimension yielding a value of 1.0 (Franzreb 1983b). Significance test: Wilcoxon Paired–sample Test.

overall trend of all species pairs considered, was for less overlap on the heavily cut stand. Franzreb (1983b) similarly noted a trend (nonsignificant) towards less overlap on logged sites, as well as a significant drop in overlap between Mountain Chickadees and Ruby-crowned Kinglets (Regulus calendula).

As a comparison, we tested the degree of overlap in the Princeton stands with those from Merritt (columns C and D, Table 8). The niche overlap between two species-pair (Mountain Chickadee/Townsend's Warbler and Chipping Sparrow/Cassin's Finch) were significantly different between Princeton and Merritt. This possibly suggests that geographical differences (in foraging repertoires and/or in the type or distribution of insect prey) may have been greater than changes in behaviour brought about by logging.

For at least those sites tested, certain bird species foraged in significantly different ways, either between-sites or between-years (Table 9). The between-site variability likely mirrored how the birds had responded to an unknown combination of differences in: vegetation; prey type, abundance and distribution; and/or species composition and densities of the avifauna. Szaro *et al.*(1990) similarly observed high between year foraging variability.

5. CONCLUSIONS

Although each species displayed preferred foraging behaviours, there were tremendous variations in their repertoires.

Birds did not utilize the forest, (in terms of those variables that were quantifiable), in proportion to the resource availabilities.

There were high levels of niche overlap between arboreal foragers, especially between morphologically similar species. High overlap may imply that strong competitive interactions occurs. However, it is just as likely that the species involved were coexisting with minimal competitive interactions, and that we had either not measured the correct habitat partitioning variable(s), or we had used too coarse a scale.

Table 9. Summary of multiple analysis of variance (MANOVA) results comparing foraging variables between sites (within same years), and between years (within same sites). Only those sites with 3 or more years of data were analyzed.

	Red-naped Sapsucker	Mountain Chickadee	Red-breasted Nuthatch	White-breasted Nuthatch	Yellow-rumped Warbler	Townsend's Warbler	Chipping Sparrow
<u>Sites 1 & 2</u>							
Between Sites	ns	p<.05	ns	insufficient	ns	ns	ns
Between Years	p<.02	ns	p<.02	insufficient	p<.01	ns	ns
<u>Sites 5 & 8</u>							
Between Sites	ns	ns	p<.05	ns	p<.01	insufficient	ns
Between Years	ns	p<.001	p<.02	p<.02	ns	insufficient	ns

Differences in forest structure brought about by logging activities failed to produce obvious foraging behaviour modifications. This may in part have been due to the high degree of foraging variability (between years, between sites and/or between individual birds), as well as to inadequate sample sizes for some species.

Vertical foraging locations and methods may have been the most important means of partitioning the forest studied.

6. ACKNOWLEDGEMENTS

We wish to thank T. Bekhuys, B. Booth, R. Heggs, A. Hetherington, B. Jedrejewska, W. Jedrejewska, C. Samper Kutschbach, P. Whitehead and D. Smith, for their assistance in collecting the field data. We also thank Weyerhaeuser Canada (Princeton) and Balco Industries (Merritt) for allowing access to the study areas. G.E.J. Smith greatly assisted in the data analysis and interpretation of the results. Our thanks go to Susan Garnham and Shelagh Bucknell who typed the manuscript.

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Appendix 1. Densities (males/100ha) by year in the eight study sites (from Morgan et al. 1989). Only those species of birds on which we collected foraging behaviour data are listed. Overall density, bird species diversity, total number of species (species richness) and density of the four main foraging guilds are also presented for each site.

	Site 1				Site 2				Site 3		Site 4
Species	1983	1984	1985	1986	1983	1984	1985	1986	1983	1984	1986
Red-naped Sapsucker	2.8	1.7	3.5		4.2	6.1	5.5		0.7	0.9	
Empidonax spp.	3.4	4.3	8.6	10.4	13.3	13.9	11.1	12.6			
Mountain Chickadee	18.2	8.2	20.5	10.2	9.8		16.5		24.0	6.1	4.1
Red-breasted Nuthatch	1.5	14.6	7.3	24.2		1.8	2.9	1.8	5.8	9.1	25.6
White-breasted Nuthatch											
Golden-crowned Kinglet	33.6	15.0	12.0	4.0	12.8				38.4	44.0	8.0
Yellow-rumped Warbler	33.1	29.3	28.8	32.8	8.4	15.7	12.6	26.7	49.9	40.9	
Townsend's Warbler	17.8	33.8	30.1	30.4		2.6	2.1	6.7	45.9	37.7	46.4
Chipping Sparrow	13.9	12.6	20.5	28.4	15.0	23.7	21.5	28.4	3.8		25.3
Cassin's Finch		8.8	8.8			7.5	4.0	3.8		1.3	
Western Tanager	38.0	21.6	38.2	33.9	3.5			2.2	5.2	2.2	21.6
Total Density	277.1	244.0	274.6	265.9	200.6	177.6	200.0	189.6	244.0	195.7	253.5
Bird Species Diversity	2.58	2.81	2.71	2.49	2.83	2.78	2.86	2.37	2.23	2.16	2.24
Species Richness	26	25	28	18	32	24	29	18	25	22	14
Ground Foragers	88.5	62.9	66.8	81.0	104.1	78.2	94.3	98.8	53.8	35.9	95.7
Foliage Gleaners	180.9	149.2	181.5	150.3	70.9	54.5	72.0	73.9	179.8	148.1	132.2
Bark Probers	4.3	23.7	10.8	24.2	8.2	10.4	16.3	1.8	10.4	11.7	25.6
Flycatchers	3.4	8.2	13.6	10.4	17.4	25.3	17.4	15.1	0.0	0.0	0.0

continued.

	Site 5			Site 6	Site 7		Site 8		
Species	1984	1985	1986	1984	1985	1986	1984	1985	1986
Red-naped Sapsucker		0.9			0.9				
Empidonax spp.	20.3	13.4	16.7	10.2	28.8	20.0	27.8	25.6	23.3
Mountain Chickadee	10.2	31.8	11.5	4.1	31.1	14.3	2.0	44.3	14.3
Red-breasted Nuthatch	3.7	1.8	19.4	12.8	9.1	20.1	7.3	5.5	33.3
White-breasted Nuthatch	4.5	1.5		7.4	1.5		7.4	1.5	
Golden-crowned Kinglet									16.0
Yellow-rumped Warbler	33.7	36.7	36.9	36.4	31.7	37.2	40.1	41.6	41.4
Townsend's Warbler	1.3			1.3		2.6	3.9		
Chipping Sparrow	33.2	39.2	26.3	17.4	47.4	40.8	45.8	38.4	44.0
Cassin's Finch	22.5	20.0	15.0	15.0	17.5	10.0	10.0	10.0	22.5
Western Tanager	10.8	19.4	38.7	13.0	17.3	29.6	8.1	39.7	33.3
Total Density	248.9	267.7	260.3	220.5	331.3	282.3	245.9	311.2	300.8
Bird Species Diversity	2.58	2.64	2.52	2.63	2.68	2.50	2.47	2.56	2.51
Species Richness	23	23	17	26	23	17	22	22	18
Ground Foragers	134.3	134.1	111.5	91.7	160.0	133.9	105.7	91.6	109.0
Foliage Gleaners	72.9	109.7	112.9	90.2	126.9	108.3	96.4	181.3	135.2
Bark Probers	10.7	6.7	19.4	22.7	11.5	20.1	14.7	7.0	33.3
Flycatchers	25.3	13.4	16.7	14.0	28.8	20.0	29.1	25.6	23.3

Appendix 2. Summary of habitat analysis results for each of the study sites.

	Site number							
	1	2	3	4	5	6	7	8
Basal Area	13.9	3.1	38.6	9.4	12.8	18.5	10.0	18.5
Canopy Volume	15899.3	2095.5	26515.8	10470.3	13306.0	14222.7	9059.2	11144.2
Tree Cover (%)	49.8	5.7	69.3	27.1	42.0	47.7	27.8	42.3
Ground Cover (%)	45.7	56.9	56.6	22.8	30.9	38.7	25.4	27.7
Log Cover (%)	4.1	3.2	6.0	6.2	2.8	2.3	5.9	4.8
Douglas-fir (no. stems/ha)	767.1	28.4	1015.8	432.8	367.9	250.3	231.1	207.2
Ponderosa Pine (no. stems/ha)	2.3	2.9	1.5	0.8	193.0	239.9	202.0	212.5
Trembling Aspen (no. stems/ha)	27.4	27.6	2.8	1.2	8.1	38.5	32.4	7.9
Other trees (no. stems/ha)	18.9	150.4	484.9	133.9	9.2	2.4	2.2	3.5
Snags (no.stems/ha)	19.7	5.7	39.5	8.5	2.8	9.2	6.2	10.1
no. live stems/ha <10.0cm (dbh)	517.9	152.5	890.7	328.6	311.2	264.9	252.5	218.4
no. live stems/ha 10.1-20.0cm	175.6	32.5	298.5	141.3	182.5	162.5	142.2	99.0
no. live stem/ha 20.1-40.0cm	105.3	11.9	209.9	58.6	66.5	65.7	58.7	64.2
no. live stems/ha >40.0cm	5.7	7.1	49.5	9.1	18.3	35.2	14.1	49.4
no. live stems/ha <10.0m tall	428.6	144.9	778.9	390.5	411.6	328.1	302.7	270.4
no. live stems/ha 10.0-20.0m tall	239.8	24.4	402.5	152.4	151.7	143.8	104.6	127.2
no. live stems/ha >20.0m tall	49.0	11.4	103.5	36.9	15.2	13.8	10.8	29.4

Note: units for Basal Area and Canopy Volume are (respectively) m^2/ha and m^3/ha. All estimates of the number of stems/ha exclude willow (Salix sp.).